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THE FIXATION OF CHARACTER IN ORGANISMS¹

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THE segregation of animals and plants into those groups which we call species, genera and families and the arrangement of such groups in a natural system of classification are made possible by the fact that during the evolution of any group there are always characters which have varied comparatively little and, from their constancy throughout large numbers of otherwise different individuals, are therefore of great value in determining relationships. Should all the characters of an individual be equally subject to change in the passage from one generation to another such chaos would result that anything but the most arbitrary classification would be quite impossible. It is of great importance to the taxonomist, the experimental morphologist and the student of evolution in general to ascertain, if possible, what are the causes for these differences in degree of variability and to attempt a formulation of the laws under which they appear.

The first attempt at a scientific explanation of this problem was put forward by the theory of Natural Selection. In its extreme form this theory assumes that all conservative characters, known to be very ancient because of their occurrence throughout large groups of organisms, are characters of supreme importance in the

¹ Graduate Bowdoin Prize Thesis in Biology, Harvard University, 1913.

struggle for existence, which have consequently been firmly standardized and kept rigidly true to type by the action of natural selection in continually eliminating those individuals which showed a tendency to depart from the normal condition. The invariable presence of segments in the Articulata, of tracheæ in insects, of the backbone in vertebrates, of gills in fishes, of feathers in birds, of roots in the vascular plants, of seeds in the spermatophytes and of vessels in the wood of the angiosperms, all of which are characters of universal occurrence in the groups which they distinguish, is explained as due to their supreme importance for survival. The frequent variability of rudimentary or obviously useless structures is laid to their unimportance in the struggle for existence and their consequent removal from the standardizing influence of natural selection. This belief in the dependence of structural conservatism on functional utility is widely held to-day and has been stated by Montgomery as follows: "A character which persists through a very long racial period must do so by virtue of being of particular value for the economy of the organization or for the perpetuation of the race. Structures of less value are more readily modified, substituted or even lost."²

A strict application of the selection hypothesis, however, evidently fails to explain many facts which a study of phylogeny brings forward. Can we imagine, for example, that either the number five, on which echinoderms are built, or the number three, which is characteristic of all hexapod insects, are or ever have been of critical value in the struggle for existence? Is it logical to suppose that the position of the protoxylem with reference to the later-formed elements of the vascular axis, a position which is extremely constant throughout the main groups of vascular plants, has been definitely determined by natural selection, or that the precise number of floral parts or the

² Montgomery, T. H., "On Phylogenetic Classification," *Proc. Philadelphia Acad. Sci.*, Vol. 54, 1902, p. 214.

particular degree of coalescence or adnation exhibited between them, is of great functional importance? Many structures, insignificant and in all probability quite useless, are extremely constant throughout large groups of animals and plants. Must we believe that all these conservative characters and structures are of immense importance in the struggle for existence, but that such features as size, shape, color and texture, which are comparatively inconstant, are of much less survival value? It is true that certain discoveries of modern physiology have lent some support to the oft-repeated defence of the selection theory that structures of apparently little importance may be in reality of much significance to the organism. Our knowledge of vital processes is as yet so slight that it is quite impossible to pronounce any particular feature as certainly of great or of little value for survival, but the mass of such information as we have acquired from a study of anatomy, physiology and ecology points decidedly to the conclusion that it is precisely those characters of little importance to the organism which are usually most conservative.

It is also very doubtful if the constancy of such apparently more essential characters as the vertebral column of vertebrates, the feathery covering of birds, or the floral reproduction of seed plants is due to the supreme importance of these characters in the struggle for existence, as the selection theory postulates; for it is evidently not the mere presence of a backbone or of feathers or of flowers *per se* which is of great significance to the individual, but the presence of these structures in very specific size, shape, texture, color and other respects. The vertebral columns of a shark and of an elephant could not be exchanged without disaster, nor could the feathers of a duck and an ostrich or the flowers of a pine and an orchid. The "conservative" character is useful only as it is associated in each individual with many other "variable" ones. The most fundamental and unalterable distinction between a fern and a flowering plant resides in their

respective methods of reproduction; but in a competition between the two it is not primarily this difference which decides the outcome. Differences in vegetative characters, as well, and in the general vigor and adaptability of the two plants determine which shall survive. One of the most conservative and deeply-seated distinctions between a mammal and a bird is the possession of hair by one and of feathers by the other, but in the struggle for existence between a bat and a night-hawk this difference is of very slight importance. The victor in such competitions is that individual all of whose bodily parts in their size, shape and general structure are so well coordinated as to produce an organism with the greatest degree of hardness and adaptability.

The conservative characters in each family or larger group—its most important distinguishing features—provide a general plan of structure, a theme, on which are produced the modifications of genera and species. It is these modifications, involving the plastic and least conservative characters, which are of most importance in adaptation and therefore in survival. The general plan is of comparatively little significance in a contest—about as much as is the particular make of modern rifle used by an army or the special type of construction of a racing car. A satisfactory interrelation and coordination of parts is the important thing, and the degree of perfection with which this is attained, on almost any plan, determines success or failure. It is true that after very long periods of time in organic evolution slight differences in value between two general plans of structure will sometimes make themselves felt and the best will finally become dominant. Seed plants have little by little overcome vascular cryptogams and mammals have superseded reptiles. A highly adaptable organism, however, constructed on an “inferior” plan will often supplant one which belongs to a generally superior type but is lacking in versatility and vigor. The common bracken fern, for example, a cryptogamous plant, is of almost universal

distribution and is much more successful than most seed plants. The great majority of fundamental distinctions and conservative characters seem to be of as little survival value as is pentamery to the echinoderms or the presence or absence of stipules to any family of the dicotyledons.

The theory of natural selection, at least in its extreme form, can not therefore well be regarded as a satisfactory explanation for structural conservatism. Darwin himself frequently called attention to the fact that "the physiological importance of an organ does not determine its classificatory value"³ and cited many examples of organs or characters obviously insignificant or useless which are nevertheless very constant and of great value in determining relationships. Darwin voices the general defence of selectionists on this point, however, when he states that "the importance, for classification, of trifling characters mainly depends on their being correlated with other characters of more or less importance."⁴

If the conservatism of a useless character depends on its correlation with one of great functional value which is continually preserved through the action of natural selection, it ought to be possible to discover this essential character and to use it in classification. A search for such universal and vitally important distinctions, however, is strangely fruitless, for in most families the only characters which we can definitely point out as common to all the individuals are precisely those which seem utterly insignificant for survival. This fact becomes increasingly obvious as we consider still broader groups where the number of common characters becomes smaller and smaller until there are but one or two features of absolute diagnostic value. The two great divisions of the amniotes, for example, the Sauropsida on the one hand and the Mammalia on the other, can be rigidly distinguished from one another only by the presence, respect-

³ "Origin of Species," 6th ed., p. 431.

⁴ *Loc. cit.*, p. 433.

ively, of one or of two occipital condyles or joints between skull and backbone. The two largest families of living conifers, the Abietineæ and the Araucarineæ, are roughly separable on several characters, but the only distinction to which no exception has been found is the presence or absence of "bars of Sanio," minute bands of pectose on the walls of the wood elements. Similarly, the monocotyledons and dicotyledons, the two great divisions of the higher seed plants, are ultimately separable, as their names imply, by the number of the cotyledons in the embryo. It can not well be claimed that any of these characters or many others which are common to wide groups of animals and plants are in themselves physiologically important but it is equally impossible to distinguish others, of great value for survival, with which these are correlated.

Darwin frequently calls attention to the fact, now so generally admitted, that a classification based on one or a few distinctions is of much less value than one which takes into account a large number of correlated characters. Such a group of characters, however, corresponds to what we have mentioned as the general plan or type of structure and consists, at least in the broader groups of organisms, of features which are mainly unimportant for survival.

It is possible to maintain that the success or failure of an organism depends more on some deeply seated property of its protoplasmic make-up, such as its powers of resistance or adaptability, than on any external and visible structures. But if there is a correlation of such fundamental abilities with features of structure, is it not more reasonable to suppose that it would occur with characters of great functional importance rather than with those which are of no physiological significance? The fact that so often in the same family, all of whose members possess the typical conservative features of the group, there are some individuals which are dominant and successful and others which are unsuccessful and are

being exterminated seems to prove that there is no correlation between the vigor and adaptability of the organism and its conservative structural characters.

Darwin maintains that the constancy of useless features "chiefly depends on any slight deviation not having been preserved and accumulated by natural selection which acts only on serviceable characters";⁵ but if all the characters and structures of any particular group were originally variable in the same degree, a supposition which the theory of natural selection is usually regarded as making, it is surely impossible to suppose that variations will not be most strikingly manifest in just those features which are not subject to the eliminating action of natural selection.

Simple and plausible as the selection theory is, we must admit that it offers by no means a complete solution of the problem of fixity since, in general, the conservatism of a structure or character seems to be inversely rather than directly proportional to its survival value. To reach a better understanding than such a theory gives as to why variation does not occur with equal frequency and extent throughout all parts of an organism, we must first of all endeavor to formulate, from the great mass of facts at hand, such general laws of variability and conservatism as we may be able to discover empirically and must then try to explain them as well as we may. A survey of the fields of taxonomy and comparative anatomy shows the possibility of discovering in the evolutionary development of organisms the presence of numerous uniformities and the operation of many general principles of phylogeny, some of which are of universal occurrence, or nearly so; others valid throughout large groups of animals and plants, and still others applicable only to particular orders or families. The formulation of such principles and a thorough application of them is the great task before the taxonomist and the phylogenist, if they are to establish their sciences on a sound and rational

⁵ *Loc. cit.*, p. 431

basis as something more than mere collections of facts. The purpose of the present paper is to set forth a few of the more important of these evolutionary principles, with their significance in the general process of evolution, and to suggest a possible explanation for the fixation of character which shall be more satisfactory than that proposed by the selection theory.

In our search for such principles of conservatism, it is primarily apparent that in the main those features which are slow to change in one family are slow to change in others also, and that consequently there are certain rather definite categories of characters which throughout all animals and plants show an inherent tendency to be conservative and slow to change, and others which are fundamentally plastic and variable. The conservative categories are, in general, those of number, relative position and general plan, characters usually of little functional significance; whereas the commonly variable features are those of more importance for survival and include such distinctions as size, shape, color and texture. The essential difference between these groups of categories is not at all in their absolute degree of conservatism or plasticity, but rather in their general tendency to become fixed or to remain plastic. Number, position and plan are not always constant, by any means, but they tend to become so during the course of evolution, whereas size, shape, color and other commonly variable characters are almost always changeable and rarely become stereotyped.

The conservatism of number is everywhere apparent. The two great groups of radially symmetrical animals, the cœlenterates and the echinoderms, are constructed (with a few exceptions) on the plans of six and of five, respectively. Insects, on the other hand, display almost invariably a scheme of three or its multiples in the number of body regions, segments, appendages and many other structures. Among fishes the number of gills, of visceral arches, of fins and of fin rays varies little throughout large families; and in the higher vertebrates, the number

of teeth, of vertebræ, of digits, of aortic arches, of brain lobes, of cranial nerves and of countless other structures is very conservative and is characteristic of large groups of animals. In the plant kingdom the fixity of number is even more noticeable. Throughout gymnospermous plants the number of sporangia to a sporophyll, in both the male and the female cones, varies but slightly. The two great groups of angiosperms, the dicotyledons and the monocotyledons, can be separated on but one constant character, the number of cotyledons in the embryo. The numerical plan of the flower in both series is also very constant, being almost invariably four or five in the dicotyledons and three in the monocotyledons. Most angiosperm families, or genera, at least, have a characteristic number of sepals, petals, stamens and carpels, which is of great importance in classification. Similar instances could of course be multiplied almost indefinitely.

Conditions of relative position and of insertion of parts are also notably conservative and of value in determining relationships. In the higher invertebrates, for example, the nerve cord is always ventral to the digestive tube and chief blood vessels, whereas in the vertebrates it is invariably dorsal. The mass of the liver may be disposed almost anywhere, but its attachment is always on the ventral side of the digestive tube. The source of the nerve supply to many organs is exceedingly slow to change and is of much importance in determining the primitive position of structures which have been moved from their original situation. Among plants, the relation of bud to leaf is very constant, and the particular relative positions of sporangium and sporophyll, of protoxylem and later-formed wood elements, and of parenchyma cells and vessels are very characteristic for each of the main groups of vascular plants. The degree of coalescence between the members of the same floral circle and the method of insertion of each of the floral circles upon the axis or upon one another are admitted to be of the greatest diagnostic value.

The character of general plan, or type, which really includes those of number and position, is of the utmost importance for the discovery of relationships. In every natural group of organisms, no matter how dissimilar its members may appear, there is always a specific plan or theme which is common to all and upon which the structure of each individual is built. The two-layered or three-layered body plan, the presence or absence of segmentation, the definite type of arthropod or vertebrate appendage which is so constant throughout its endless modifications, the plan of the central nervous system in the vertebrates, and the precise and unvarying character of the epidermal structures in the different classes of that phylum, are a few of the innumerable examples of the conservatism of type in the animal kingdom. In the case of plants the same fact is no less evident. The general topography of the vascular system, the presence or absence of leaf-gaps, the degree of differentiation in the structure of the wood and the open or closed character of the leaf venation are all extremely constant. The notable conservatism of type in the reproductive organs of all plants is well known and is universally used in classification. The almost complete uniformity throughout animals and plants of many cytological characters, such as those concerned with mitosis, might also be cited as striking examples of the conservatism of plan or type.

Plastic and variable characters, no less than conservative ones, are separable into categories, the most important of which are size, shape, color and texture, of which the inconstancy is so notorious that any broad classification based upon them is very rarely a natural one.

But even if we admit that certain characters are essentially more slow to change than others, it is very evident that this difference is not an absolute one, but that "conservative" features may display a greater or a less degree of constancy in certain parts of the organism than in others. These differences in local variability, however, like those between general categories of characters, are

not random and entirely unpredictable ones, for we are able to distinguish certain definite parts of the plant and animal body which throughout larger or smaller groups of organisms are characteristic seats of conservatism, and others which are everywhere subject to continual change. The urinogenital, nervous and skeletal systems of vertebrates, and to a certain extent of invertebrates as well, are typically conservative and subject to comparatively slight alteration during evolutionary development. Certain definite regions of the body, such as the skeleton of the mammalian neck, are more definitely stereotyped than others as to the number and arrangement of parts. The extreme conservatism of the reproductive organs of all plants has of course long been recognized and has been proven by a study of internal as well as of external structure. More recently it has been demonstrated, that the woody axis, as well, is the seat of firmly fixed and therefore ancient characters. Each main division of the vascular plants has a fundamental stelar plan, and every subordinate group has its peculiar and specific type of wood structure which is exceedingly constant in individuals otherwise very different and, as a diagnostic character for families and sometimes smaller groups, is therefore of much value. The axis of the root is especially conservative and has remained practically unchanged in its general plan throughout the entire evolution of woody plants. The vascular system of the leaf, especially at the node where the leaf and stem unite, has many times been found to display primitive features wholly lost elsewhere. In such conservative systems and regions it is not *all* the characters which have become constant, but only those which we have called typically conservative, such as number, position and plan. Variable characters are variable anywhere.

Not only are certain regions of the body characteristically more conservative than others, but it is also true that particular stages, notably the earlier ones, in the life history of the individual are much less subject than the

rest to variation and change. The law of recapitulation, which declares that ontogeny repeats phylogeny, is now accepted in a more or less modified form by almost all zoologists, and despite differences in the interpretation of embryology as a guide to a knowledge of ancient animals, it is generally agreed that early developmental stages are much more conservative than are later ones.

Not as many striking examples of recapitulation are known among plants as among animals, but Darwin long ago noticed resemblances between the leaves of certain seedlings and of their supposed ancestors, and others have cited many similar instances. Attention has more recently been called, particularly by Jeffrey, to the fact that the internal structure of the young plant or of a first annual ring of the mature plant, even more clearly than their external form, is slow to change and therefore frequently displays primitive characters. The woody axis of one of the higher ferns begins in the sporeling as a solid rod, which, after forming a medullated cylinder, gives rise to the complicated vascular system of the adult, the various steps of its development representing stages through which its ancestors doubtless passed and which now characterize the more primitive living families of ferns. In the first annual ring of certain conifers occur resin canals, "bars of Sanio," parenchyma cells and other structures present throughout the wood of more primitive and presumably ancestral types. The first few annual rings of many angiosperms, as well, show in the structure of their rays and vessels characters which are undoubtedly ancient. On an abundance of such evidence as this it must be admitted that the validity of the law of recapitulation has been demonstrated for plants almost as thoroughly as for animals.

We have seen that conservative characters vary considerably in their constancy according to the part of the body or the stage of development with which they are associated. Still more notable cases of differences in fixity are evident in similar characters occurring in different fami-

lies. A feature which is conservative and of diagnostic value in one group may be variable and worthless in another. The number of teeth and vertebræ, for example, is much less constant among fishes than among mammals. The general floral plan is far from uniform throughout the Rosaceæ, but in such families as the Cruciferæ it is exceedingly constant. This introduces still another principle of conservatism which is really the crux of the whole problem of fixation of character and seems to be a fundamental law of evolution—the principle that the progressive evolution of any character or structure, whether involving reduction or increased complexity, is attended by a continual decrease in its tendency to change. Differentiation and specialization are followed by increasing fixity.

It is a well-known biological fact that the more primitive families of animals and plants, those which still maintain an ancient type of organization, are much more variable in their characters than are those which have progressed far from such a primitive condition. The lower Arthropoda, for example, display great variety in the number of body segments and appendages and in many anatomical features, but the highly specialized hexapod insects, despite their enormous numbers, wide distribution and extreme variation in size, shape and color, have become rigidly stereotyped with regard to almost all characters of number and general plan. In the ascending vertebrate series from cyclostomes to mammals there are also many instances of the increasing fixation of what we have called conservative features, for it is well known that the characters which make up the mammalian type are much more definite and sharply circumscribed than those pertaining to the lower groups of vertebrates where there is much latitude in the distinguishing features. Likewise, the most advanced and highly specialized families of plants, such as the Compositæ and the Orchidaceæ, are characterized by a stereotyped floral plan which is invariable throughout all the members of these dominant groups, whereas in plant orders admittedly lower in the scale, such as the

Rosaceæ, Caryophyllaceæ, Cyperaceæ and Gramineæ, the floral type is very much more various both in number and in relative position of parts. The evolution of the gametophyte from its gymnospermous to its angiospermous condition is a continual progress from simple and variable structures to those which are fixed and highly specialized. The same principle is evident as well among vegetative structures, for the lower and more "generalized" families, both among conifers and dicotyledons, show a greater diversity in their wood structure than do the higher groups.

This progressive evolution from a primitive variable condition to one which is fixed and specialized is always attended by a reduction in the number of similar parts. Multiple structures are characteristic only of the lower types of organization. Other characters tend to show a similar phylogenetic change from the complex to the more simple, with the result that a structure in its highly developed state is very often less complex than is its more primitive homologue. Evolution more often involves reduction than amplification.

These four general principles of conservatism—that there are definite categories of fundamentally conservative and fundamentally variable characters; that certain organs or regions of the body are more conservative than others; that early stages in ontogeny are more constant than later ones, and that advance in evolutionary development involves an increase in fixity, are established on a large and continually increasing mass of observed facts and may well demand recognition from all biologists. Many other principles, such as those concerned with reversion and orthogenesis, are gradually being formulated and it is only a matter of time and more extended observation before the science of phylogeny will be placed on a much more uniform and exact footing.

To establish these laws on a sound basis of observed facts is a matter of some labor, but it is a much less difficult undertaking than to provide a reasonably complete

explanation for their existence. This task must ultimately be left to the sciences of physiology and genetics, and in the meantime it is possible only to make suggestions and conjectures as to what are the causes which underlie the facts of conservatism.

The very difficulties in the way of the explanation of fixity proposed by the theory of natural selection suggest a possible solution of one of the most conspicuous problems—why it is that just those characters of least physiological importance and survival value are most conservative. May it not be true that the tendency toward progressively increasing fixity, which seems to be almost universal in organic evolution, has succeeded in rendering comparatively invariable those features which are of little significance for survival, but that in the case of vitally important characters this tendency has been overcome by the opposing action of natural selection in eliminating individuals which are not sufficiently plastic and adaptable, and in thus maintaining or increasing the variability of all characters important in the struggle for existence?

If this conception of the matter is a true one, the function of natural selection is almost precisely the reverse of what it is ordinarily supposed to be, for instead of operating to fix characters and preserve types intact its action results in their elimination, in so far as they interfere with success, and in the placing of a premium on versatility. Selection, in other words, is made for general adaptability under varying conditions rather than for the possession of any particular characters or structures. The great variability of dominant organisms, long ago noticed by Darwin, should be regarded on such a hypothesis as a cause rather than a result of their dominance. Fixity is tolerated by natural selection only so long as it affects characters of little or of no functional importance. Such characters thus become very conservative and furnish the taxonomic “type.” This conception of organic evolution as the result of the continual inter-

action of these two great factors—progressive fixation, which is ever tending to make characters constant and to decrease variability; and natural selection, which operates in eliminating individuals which have become too rigid in their vitally essential features, and thus in encouraging those which display superior adaptability—is at least helpful in presenting a clear picture of the process of evolution.

The marked conservatism which we have noticed in particular structures or organs may perhaps be explained in a similar way as due to their comparative unimportance in the economy of the individual. The fact that the reproductive organs in all plants and in many animals are especially conservative may possibly be taken to indicate that the particular method of reproduction is of less vital concern to the race than are its other activities. The conservatism of other structures, such as the root, is evidently due to the comparative constancy of their surroundings. Internal structures in general are apt to be more conservative than external ones because of their exposure to a less varied environment.

Various attempts have been made to explain those phenomena of conservatism which have been grouped under the head of recapitulation. De Vries has maintained that the seedling characters of plants are just as dependent on the action of natural selection as are those of the adult and that ancient features persist in youth only when they happen to be of survival value for the early stages of the plant. The same position has sometimes been maintained on the zoological side. To attribute functional importance to all embryological characters, however, and to explain the numberless cases where there is close correspondence between ontogeny and ancestry as due simply to the operation of natural selection, is to burden that hypothesis beyond all necessity.

The theory of formative stimuli, which explains the persistence of structures in the embryo of animals on the assumption that their presence is absolutely necessary as

a "stimulus" for later development, meets with difficulties in the case of plants. Here development is not due to interstitial growth, as in animals, and does not involve progressive differentiation of almost all the cells of the body, but is brought about by the activity, at a growing point, of a small group of undifferentiated, continually dividing cells, from the innermost of which are laid down tissues which almost immediately become fixed and unalterable in size and shape. The influence, upon such a distant growing point, of structures previously laid down must be slight as compared with the effect of already formed structures, in animals, upon growth in which they themselves are taking an active part.

The facts of recapitulation can perhaps be understood better on the principle, which we have already discussed, that certain categories of characters are inherently more conservative than others. It may be said that, theoretically, every individual tends to inherit all the peculiarities of its ancestors; but since life is short and history is long, most of the chapters have to be omitted. It is only reasonable to suppose that those features will disappear first during evolutionary advance which are least conservative and least firmly fixed in the constitution of the race; and such we find to be the fact, for it is not characters of size, shape, color and texture which are usually preserved in ontogeny, but the less plastic ones of number and plan. The presence of gills and their associated skeletal and circulatory structures became rigidly implanted in the primitive vertebrate stock and the general outline of these structures still persists in the embryos of modern terrestrial forms. It is not a functional gill which is repeated, however, nor one of definite shape or special construction, but simply a gill cleft, with the vestiges of its ancient skeleton and vascular supply. It is as though what the geneticist would call the factor for the gill openings had persisted unchanged, but that the factors for the shape, size and structure of the gills had been widely altered or disappeared altogether. The developing axis

of a woody plant repeats little of the histological features of its predecessors, but it does recapitulate the general vascular topography of successive ancestral forms. The developing organism has concentrated within it an essence, so to speak, of the most conservative and therefore the most salient characters which distinguished the ancient members of its line. The fact that all plastic and highly variable features have been swept away enables these historical landmarks to stand out distinctly, and gives to the structure of the animal embryo and of the young plant a very important significance in the science of phylogeny.

The principle that fixity of character increases with differentiation, which we have regarded as of so much importance in evolution, is easier to establish than to explain. It is possible to regard the matter from the viewpoint of genetics and to imagine that a "variable" species is a "mixed population," the members of which are continually intercrossing, and that the appearance, in certain individuals, of definite discontinuous variations isolates such individuals from the rest of the species and causes the partial or complete establishment of each as a distinct "pure line" with more closely defined characters. The more numerous such discontinuous variations were, the more complete the isolation of a given line would become and the more purely, therefore, would it reproduce itself until finally its characters became very sharply fixed. In other words, fixity may be due to germinal segregation and may depend directly on the proportion of factors which are in a homozygous condition in the germ plasm of the two parents. Complete homozygosity in both would ensure complete fixity of parental characters in the offspring.

A comparison also suggests itself between the effects of differentiation in ontogeny and in phylogeny. Experimental work has shown that in the more primitive animals, where the power of regulation is best developed, any part of a tissue or elementary organ, so long as it remains

undifferentiated, is able, upon necessity, to give rise to all structures that the whole tissue would normally have produced. A sufficiently large group of cells from any portion of the blastula of an echinoderm, for example, will produce a normal larva; but the moment the process of gastrulation begins, this power of producing the whole animal is definitely lost by those very cells which possessed it but a few hours previously; for, now that differentiation has begun to take place, a piece which shall give rise to a normal larva must include a little of both the primitive ectoderm and entoderm and can not be taken at random from anywhere in the embryo. Any portion of the primitive gut, which later develops, is able to produce the coelomic pouch, should the normal region of origin of that structure be removed, but this "equipotency" lasts only so long as there is no differentiation, for if the pouch once begins to develop and then is removed it can never be produced again even by the cells which a short time previously had the power to form it. This process of ontogenetic segregation results in the continual loss of potentialities, in the progressive narrowing down of the possibilities at the command of every living cell. The situation in phylogeny is very similar, for the possibilities before a simple, plastic and comparatively undifferentiated organism—the lines of evolution along which its descendants may go—are much greater than those before one which is highly developed and sharply specialized. Increased differentiation is followed so regularly by decreased plasticity, both in phylogeny and ontogeny, as to suggest the possibility of a common cause.

There is also a similarity between structural fixation and certain psychological phenomena. The performance of an action is always uncertain and variable at first, but constantly tends to become stereotyped and habitual. The simpler types of animal activity are directed by instincts which are comparatively changeable and plastic, but where behavior has become highly specialized and complex, in-

stinct has attained a high degree of precision and invariability. In the same way, a person whose activities are of wide range and comparative simplicity is much more adaptable than one who has become habit-bound through a life of intense specialization. As an organism's "experience mass" becomes continually greater and more complex the formation occurs of that system of habits which in man we call a mental character, and this process, like that of ontogenetic and phylogenetic development, involves the continual elimination of potentialities and consists in the progressive fixation, with advancing age, of characters which during youth were variable and inconstant. It so much resembles the establishment of an organic structural type by the elimination of variability through advance in specialization as to suggest that perhaps both phenomena are manifestations of the same cause.

Such attempted explanations of the differences in fixity which occur between organic characters are of course incomplete and highly unsatisfactory. The very fact, however, that it is possible at all to formulate principles of conservatism and variability, unexplained though they may be, which shall be of application throughout the animal and plant kingdoms or which shall at least be operative in certain definite groups of organisms, is of great significance and value to the biologist, for it enables him to place all branches of his science on a somewhat more exact and uniform basis. It must of course be borne in mind that such principles as these are not invariably operative, for exceptions to all of them are frequently found. Biological laws undoubtedly exist, but they seem to belong to quite a different category from the invariable ones of the physical sciences.

The science of taxonomy will perhaps receive the greatest benefit from a general recognition of the fact that there are such things as laws of phylogeny, for a united effort by all biologists to define these laws more clearly and to apply them more widely will result, through the

establishment of much more precise taxonomic criteria, in a clearing up of many difficulties and disputes as to relationships and in the construction of a truly natural classification on a more logical and consistent basis.

A knowledge of phylogenetic principles is also of value to the general student of evolution, for through it a better conception of the development of organic structures may be obtained than is set forth by the selection theory. A recognition of the facts that fixity increases with differentiation and that there are inherent differences in variability between functionally important characters and those which are useless for survival makes possible a much clearer understanding of the evolutionary history of any particular group.

The evolution of the hexapod insects is a case in point. The primitive insects seem to have been air-breathing arthropods with an indeterminate number of body segments and appendages. The ancestors of our modern hexapods achieved their first success through some advance in specialization over this more primitive type, but the improvements which gave them ascendancy and which enabled them to found a distinct and dominant group were certain unknown changes, doubtless in plastic and functionally important characters which were of great value for survival at the time, but which, having isolated the family and put it on its feet, so to speak, continued to change and may be possessed by few or no living descendants. The progressive increase in specialization, however, which caused the success of the primitive hexapods resulted in the gradual fixation of certain functionless characters, such as the number of segments and appendages, which finally became rigidly stereotyped as we see them to-day, so that they now distinguish *all* hexapods, whether successful and dominant species or those which are being beaten and exterminated. The conservative features have progressed steadily but slowly to their present condition, but the plastic characters, during the same time, have doubtless passed through wide and unre-

corded ranges of variation and in so doing they have, as it were, caught and fixed into the advancing and increasingly specialized hexapod type the particular conservative and functionless characters which happened to distinguish those fortunate individuals which founded the present family. As a result our modern hexapods, as a whole, like all other natural orders, have as constant characters certain peculiarities of number and plan, whereas the subordinate groups of the order are still distinguished, in many cases, by the functionally important features to which they owe their successful establishment, but which in future evolution are doubtless destined to vary much.

Similarly, in that ascending group of animals which were to give rise to the higher vertebrates, the primitive archipterygium became stereotyped into the pentadactyl appendage, with its definite skeletal plan; but the particular improvements which caused the primitive pentadactylous stock to succeed at the start and to become segregated as a new and distinct order were doubtless concerned with such plastic but functionally important characters as size and shape and with the general vitality and adaptability of the race, and had little or nothing to do with the particular number of digits or arrangement of bones in the appendages. These characters, originally variable, simply happened to belong to a successful and progressive group of organisms and became fixed and stereotyped as specialization took place.

The ancestors of the grasses doubtless varied much as to nodal structure, but the particular group which through its success became the dominant and distinct modern family happened to be characterized by the possession of leaves whose bases formed an open sheath around the stem and were provided with a small membranous structure, the ligule. These characters, which are doubtless not the ones to which the family owes its success, since they are present alike in dominant and in unsuccessful species, became so firmly fixed during the progressive evolution of the Gramineæ that they now distinguish all members of the family.

All conservative and stable characters which are common to large groups of organisms have thus reached their present condition through slow but steady progress during the same time that plastic and functionally important features were changing and moulding themselves in adaptation to every new demand of the environment.

Organic evolution in general, including that of human civilization, seems to have resulted from the opposing actions of the two great factors which we have so often mentioned: on the one hand, the tendency toward fixation, which results in the stereotyping of structures and of habits and social customs, and which gives rise to mental as well as physical conservatism; and, on the other, the action of natural selection in weeding out such physical characters as tend to make the organism unadaptable and such customs, institutions and even societies as have become too firmly stereotyped through habit and precedent or too bound by tradition to maintain themselves in the advance of civilization. Natural selection does not interfere with useless or harmless characters which therefore become firmly fixed and are of great value in determining relationships between organisms and between civilizations and in deciphering the path of evolutionary advance.

This biological principle that trivial but conservative characters which happen to distinguish the beginnings of a successful evolutionary line become closely associated with all its subsequent development has therefore many suggestive parallels in human history. Any great movement is always colored by the circumstances surrounding its inception. The fact that our first popular translation of the Bible happened to be written in the seventeenth-century English does not account for the enormous subsequent spread of the Scriptures, but nevertheless the now archaic phraseology of the King James Version, a "conservative character" like all religious phraseology, and "unimportant for survival," has persisted almost unaltered throughout the history of the Protestant churches,

and, surviving numberless changes of ritual, creed and theology, has stamped itself indelibly upon religious expression everywhere.

The whole subject of organic conservatism is so vast and so little understood as to be far beyond satisfactory treatment within the limits of such a paper as the present one. An extensive correlation of the mass of facts already in our possession and the discovery of a multitude of new ones will be necessary in order to formulate laws of phylogeny with any degree of accuracy. The essential point in the whole matter is the indication that evolution of animals and plants is not a random and fortuitous process, dependent on the caprice of external, inorganic nature, but that it is subject everywhere to certain definite and discoverable laws. Such a point of view, of course, is essentially an orthogenetic one and emphasizes the importance of the evolving organism rather than the creative power of the environment. By establishing the essential uniformity of vital processes everywhere it also tends to elevate biology from a mere subsidiary of the physical sciences to an independent position of its own.

SUMMARY

1. The construction of a natural classification of organisms is made possible only by the fact that certain characters of every individual are more conservative and less subject to variation than others during evolutionary development.

2. The explanation of conservatism propounded by the theory of natural selection is unsatisfactory since, so far as we are able to determine, characters which are most firmly fixed are in general those of least importance for survival.

3. From a study of phylogeny it is possible to formulate certain general principles of conservatism which are valid throughout more or less extensive groups of organisms.

4. The principal categories of conservative characters are those of number, position and plan.

5. Particular organs or regions of the body, throughout large groups of animals and plants, are less subject to change than others and hence are seats of primitive characters.

6. The early ontogenetic stages of animals and plants repeat those characters which were most conservative and firmly fixed in their ancestry.

7. Evolutionary advance and increase in differentiation tend to result in the decrease of variability. This is analogous to the loss of potentialities during ontogeny and is also comparable to the formation of habit.

8. Organic evolution is dependent on the action of two opposing factors: that of progressive fixation, which tends universally toward greater rigidity and conservatism in all characters during evolutionary advance; and that of natural selection, which tends to maintain or increase the variability of those characters important for survival by eliminating individuals where such characters have become so fixed that the organism fails to possess a necessary degree of adaptability. Natural selection is not concerned with harmless and trivial characters which consequently tend to become very conservative and are of much value in classification.

9. Such general principles of phylogeny as these, if thoroughly established and defined, will make possible the construction of a truly natural classification of organisms on a logical and uniform basis. They also present a clearer conception of the general method of evolution than is set forth by the theory of natural selection alone.

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